UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFETS RÉGIONAUX, SPÉCIFIQUES ET ALLOMÉTRIQUES SUR L'OUVERTURE DE LA COURONNE DU BOULEAU JAUNE, DE L'ÉRABLE À SUCRE ET DE LA PRUCHE DU CANADA: IMPLICATION POUR LA PARAMÉTRISATION DU MODÈLE SORTIE.

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AVANT-PROPOS

Ce mémoire présente mes travaux de maîtrise et est composé de deux chapitres. Ils sont tous deux présentés sous la forme d'articles, où Marilou Beaudet et Christian Messier sont second et troisième auteurs respectivement. Ayant été responsable du projet sur le terrain, de l'analyse des données et de la rédaction je figure comme première auteure pour les deux manuscrits. Marilou Beaudet a participé à l'élaboration de la méthode, m'a enseigné les techniques d'analyse de photos numériques et a participé aux analyses statistiques, tandis que Christian Messier a assuré la supervision du projet ainsi que son financement. Le premier chapitre porte sur la variabilité de l'ouverture de la couronne chez l'érable à sucre, le bouleau jaune et la pruche du Canada selon certaines caractéristiques des individus, des espèces et des sites. Ce manuscrit sera soumis à la Revue canadienne de recherche forestière en octobre 2006. Le second chapitre est un compte rendu de la paramétrisation du module de lumière du modèle SORTIE, pour les régions du Témiscamingue, de Haliburton (Ontario) et de la péninsule supérieure du Michigan (Nord et Sud), pour les mêmes espèces. Après avoir complété ce chapitre, entre autre en utilisant le modèle pour effectuer des prédictions de lumière en sous-bois, nous serons en mesure de soumettre cet article, toujours à la Revue canadienne de recherche forestière, au début de l'année 2007.

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RÉSUMÉ

L'ouverture de la couronne (OC) des arbres matures influence grandement la transmission de la lumière au travers de la canopée forestière. Pourtant, dans le contexte de modélisation de la lumière en milieu forestier l'OC est souvent considérée constante à l'intérieur d'une espèce, peu importe les dimensions de l'individu ou sa provenance géographique. L'objectif de cette étude est de tester si l'OC est constante pour le bouleau jaune (*Betula alleghaniensis* Britton), l'érable à sucre (*Acer saccharum* Marsh.) et la pruche du Canada (*Tsuga canadensis* (L.) Carr.). Plus spécifiquement, l'influence des facteurs suivants a été testée : 1) le diamètre à hauteur de poitrine (DHP), 2) l'angle de transmission de la lumière par rapport au zénith, 3) l'allométrie de la couronne et 4) l'évapotranspiration potentielle. Les valeurs d'OC ont été obtenues pour 380 individus à partir de photos numériques de couronnes (à 0°, 15°, 30°, et 45° du zénith) en suivant la méthode utilisée par Beaudet et al. (2002). Les résultats suggèrent que l'OC diffère selon l'angle de transmission de la lumière ainsi qu'en fonction du ratio diamètre de la couronne/diamètre au tronc, et qu'il y a interaction entre ces deux facteurs. Tandis que les arbres dominants peuvent intercepter la lumière latéralement (e.g., 45°) et verticalement (e.g., 0°), les petits arbres sont beaucoup plus efficaces pour intercepter la lumière verticale plutôt que latérale. Ceci suppose une distribution initialement planophile du feuillage chez les petits arbres, suivie d'une transition vers une distribution aléatoire de l'angle des feuilles au fil de l'ontogenèse. L'augmentation de l'évapotranspiration est associée à des couronnes plus ouvertes. De façon complémentaire à ces observations, le module de lumière du modèle SORTIE a ensuite été paramétrisé (allométrie et OC). Les différences entre les régions sont généralement plus marquées pour l'OC que pour les paramètres allométriques, mais l'impact de ces différences sur les prédictions de lumière n'a pas encore été testé. Il serait nécessaire de mieux comprendre la variabilité de l'OC avant de l'intégrer dans les modèles de simulation de la dynamique forestière.

Mots clés : Ouverture de la couronne, allométrie, évapotranspiration potentielle, SORTIE.

INTRODUCTION GÉNÉRALE

Dans le biome de la forêt tempérée décidue, comme dans plusieurs autres biomes, la lumière est une ressource clé, qui détermine en partie quelles seront les espèces arborescentes dominantes (Yude *et al.*, 2002). En sous-bois, l'hétérogénéité lumineuse est cruciale pour la régénération, car elle permet à des espèces avec différents degrés de tolérance à l'ombre de coexister; les espèces plus opportunistes et moins tolérantes à l'ombre étant avantagées par les trouées tandis que les espèces tolérantes peuvent croître sous la canopée. La reconnaissance de ce phénomène a mené à une meilleure compréhension du fonctionnement des écosystèmes forestiers en reconnaissant le rôle important joué par la dynamique des trouées (Runkle, 1985; Canham, 1988; Canham *et al.*, 1990). Par contre, une grande variabilité dans la transmission de la lumière peut aussi être expliquée par les caractéristiques du couvert (Canham *et al.*, 1994; Wirth *et al.*,2001).

Depuis les travaux de Monsi et Saeki (1953), la loi de Beer-Lambert est couramment utilisée afin de calculer l'interception de la lumière dans la canopée forestière. Les postulats sont les suivants: les feuilles 1) ne reflètent et ne transmettent aucune lumière et 2) sont distribuées aléatoirement dans le volume de la cime. Or il est connu que ces postulats ne sont souvent pas respectés en forêt (Statd et Lieffers, 2000; Sinoquet *et al.*, 2005). Le non respect de ces postulats peut être pris en compte en ajoutant certains paramètres à l'équation de Beer-Lambert (par exemple, un coefficient de correction pour l'agrégation du feuillage). Il n'en demeure pas moins que même si la transmission de la lumière peut être modélisée par la loi Beer-Lambert dans la plupart des peuplements purs, équiens et dont la canopée est

relativement uniforme, il demeure complexe de calculer ou de modéliser la transmission de la lumière pour un couvert hétérogène, multi-étagé et comportant de multiples espèces. Dans le cas de canopées hétérogènes où sévit un régime de trouées (e.g. en forêt tempérée décidue), la ressource lumineuse en sous-couvert peut être très variable. À l'échelle du peuplement, certains modèles spatialement explicites rendent compte de cette hétérogénéité lumineuse en sous couvert grâce à une représentation individuelle des couronnes et à la simulation des trouées (e.g. SORTIE, MIXLIGHT, tRAYci) et représentent des outils intéressants et applicables à l'aménagement. Toutefois, le processus de transmission de la lumière au travers des couronnes est souvent représenté de façon simplifiée dans les modèles: on utilise communément une seule valeur de coefficient d'extinction par espèce, peu importe les caractéristiques des individus (grandeur, statut social dans le peuplement). De plus, l'extrapolation des prédictions de ces modèles d'une région à l'autre représente un réel problème (Lieffers *et al.*, 1999; Stadt et Lieffers 2000; Sonohat *et al.*, 2004) étant donné que la variabilité entre les sites n'est souvent pas considérée dans la paramétrisation.

Il est connu que la transmission de la lumière change selon certaines caractéristiques de la canopée (Lieffers *et al.*, 1999; Beaudet *et al.* , 2002). À l'échelle de l'arbre individuel, la tolérance à l'ombre, l'allométrie de la cime, la densité foliaire, l'agrégation foliaire ainsi que l'angle des feuilles sont tous des facteurs qui peuvent modifier la transmission de la lumière. À l'échelle du peuplement, le régime hydrique et les conditions climatiques qui pourraient avoir un effet sur la transmission de la lumière en modifiant les caractéristiques nommées précédemment.

Les observations de Horn (1971) suggérant que les espèces tolérantes à l'ombre ont une capacité supérieure à intercepter la lumière comparativement aux espèces mi-tolérantes ou intolérantes ont été confirmées par plusieurs auteurs

(Canham *et al.*, 1994, 1999; Messier *et al.*, 1998; Lieffers *et al.*, 1999; Beaudet *et al.*, 2002; Kitajima *et al.*, 2005). Ceci peut s'expliquer par des couronnes plus longues pour les arbres tolérants ainsi qu'une surface foliaire plus élevée (Canham *et al.*, 1994; Aiba et Kohyama, 1997; Sterck *et al.*, 2001; Kitajima *et al.*, 2005). Le maintient de branches basses et de feuilles au centre de la couronne est rendu possible chez ces espèces par le fait que celles ci ont un point de compensation photosynthétique inférieur (Givnish, 1988). Pour les mêmes raisons, les espèces intolérantes ont tendance à garder les feuilles en périphérie de la cime afin de réduire la densité foliaire au centre du volume de la couronne. Il est préférable de tenir compte de ce phénomène lorsque des prédictions sont faites avec les modèles de transmission de la lumière (Canham *et al.*, 1994; Brunner, 1998).

L'allométrie des arbres individuels et particulièrement de leur cime peut aussi influencer l'interception de la lumière. Nous avons vu que la longueur de la cime peut augmenter l'interception de la lumière au niveau de l'individu. Par contre, si dans un peuplement les individus investissent peu dans la largeur de la couronne, comme c'est le cas quand il y a abrasion des couronnes (Rudniki *et al.*, 2004), il peut y avoir plus de lumière pénétrant en sous-couvert. Étant donné que la fermeture de la canopée à l'échelle du peuplement dépend en partie de la capacité des individus à occuper l'espace disponible avec leur couronne, le rayon de la cime s'est révélé être une variable cruciale dans la modélisation de la transmission de la lumière, tant en forêt boréale (Stadt et Lieffers, 2000) que feuillue (Beaudet *et al.*, 2002).

La distinction entre les arbres de différentes dimensions ou qui occupent différents étages dans la canopée n'est souvent pas considérée en modélisation. Pourtant, ces éléments peuvent expliquer certaines différences dans la capacité des arbres à transmettre la lumière. Par exemple, un arbre dominant occupant la strate supérieure de la canopée pourra, avec une couronne élargie, intercepter beaucoup de

lumière. On observe ainsi généralement une transmission de la lumière moindre chez les arbres plus grands (Martens *et al.*, 2000; Kitajima *et al.*, 2005). Pourtant, il est aussi connu que les arbres supprimés sont efficaces pour intercepter la lumière provenant du zenith (Niinemets *et al.*, 2005; Niinemets *et al.*, 2004) grâce à une orientation préférentielle des feuilles à l'horizontale (Givnish, 1988; Horn, 1971). Falster et Westoby (2003) ont distingué des espèces d'arbres selon leur efficacité à intercepter la lumière verticale ou latérale et ont observé que l'angle des feuilles influençait grandement cette efficacité.

La transmission de la lumière peut donc varier au sein d'une même couronne (Barclay, 2001; Werner *et al.*, 2001; Falster et Westoby, 2003; Niinemets *et al.*, 2005) car la distribution des feuilles dans le volume de la couronne, leur densité ainsi que leur angle d'inclinaison sont tous des éléments déterminant la transmission de la lumière. Ces variables font souvent partie intégrante du coefficient d'extinction utilisé dans la loi de Beer-Lambert (Brown et Parker, 1994; Larsen et Kershaw, 1996; Brunner, 1998; Stadt et Lieffers, 2000, 2005).

L'angle des feuilles peut être un facteur important affectant la transmission de la lumière (Utsugi, 1999; Barclay, 2001) et peut changer au sein de la couronne et varier entre les individus. En général, l'inclinaison diminue du haut en bas de l'arbre, i.e. que les feuilles sont plutôt orientées verticalement au haut de la cime et horizontalement dans le bas de la cime (Utsugi, 1999; Barclay, 2001; Falster et Westoby, 2003). L'angle des feuilles varie aussi en fonction de l'ontogenèse et selon l'environnement lumineux (Utsugi, 1999). De cette façon, les feuilles de lumière ont une inclinaison plus marquée qui leur permet de capter la lumière de l'horizon au zénith, ainsi que de minimiser la photoinhibition et l'auto-ombrage, tandis que les feuilles d'ombre adoptent une orientation horizontale afin de maximiser l'interception de la lumière (Givnish, 1988; Falster et Westoby, 2003). Cette distinction existe aussi

au niveau de l'espèce car les arbres tolérants à l'ombre ont une distribution plus planophile du feuillage que les intolérants (Barclay, 2001). Même si la variabilité de l'angle des feuilles est connue, on assume souvent une distribution aléatoire de l'angle des feuilles en modélisant la transmission de la lumière en sous-bois (Stadt et Lieffers, 2000; Werner *et al.*, 2001).

La densité foliaire (ou leaf area density, LAD) est une autre variable qui affecte grandement la transmission de la lumière selon Stadt et Lieffers (2000) et Sinoquet et al. (2005). Cette variable est parfois généralisée à l'espèce et parfois même au site, dépendamment du caractère homogène du peuplement (Gersonde *et al.*, 2004; Piboule *et al.*, 2005). Les variations dans la densité foliaire s'expliquent par l'agrégation (ou clumping) de feuilles autour de certaines branches, ce qui peut induire une transmission de lumière plus élevée étant donné les vides résiduels qui se trouvent dans la couronne. Ce phénomène est surtout observé chez les arbres plus vieux avec un indice foliaire (ou leaf area index, LAI) plus élevé (Kucharik *et al.*, 1999; Niinemets *et al.*, 2005) et pourrait expliquer la transmission de la lumière plus élevée que l'on observe dans les forêts surannées (Brown et Parker, 1994; Frazer *et al.*, 2000).

On a souvent recours en modélisation, afin de caractériser les propriétés de transmission de la lumière des arbres, à un coefficient d'extinction (Stadt et Lieffers, 2000; Gersonde *et al.*, 2004) ou, dans le cas de du modèle SORTIE, à une valeur d'ouverture de la couronne (OC) (Canham *et al.*, 1994; Beaudet, Messier et Canham, 2002) qui ne varie que selon l'espèce. Cette variable réfère à la fraction de vide que l'on retrouve dans la couronne (Astrup et Larson, 2006) et est mesurée à l'aide de photos hémisphériques ou de simples photos numériques. Même si cette variable représente bien la transmission totale de lumière à l'échelle d'une couronne individuelle, le fait qu'elle soit généralisée à l'espèce a pour résultat qu'on ne tient

pas compte des variations dans les propriétés de transmission de la lumière entre individus selon leur grandeur ou leur dominance dans la canopée. Toujours dans le cas du modèle SORTIE, les couronnes sont représentées par des cylindres et la variation allométrique de ceux-ci n'affecte pas l'ouverture de la couronne (OC). Par contre, il est probable que les individus d'une même espèce, petits ou grands, supprimés ou dominants, n'interceptent pas la lumière de la même façon.

De plus, on ignore à quel point la capacité des arbres à intercepter la lumière peut être généralisée géographiquement. Ce phénomène est fréquemment soulevé lors de l'interprétation des prédictions de lumière en sous-bois (Sonohat *et al.*, 2004; Stadt et Lieffers 2000; Lieffers *et al.*, 1999) car il constitue une limite considérable à l'applicabilité des résultats. Même si jusqu'à maintenant les études menées par Sonohat et al. (2004) et Stadt et al. (2005) n'ont pu démontrer l'effet du site sur l'interception de lumière, l'influence du régime hydrique, et particulièrement de l'évapotranspiration sur la surface foliaire est connue (Gholz, 1982; Woodward, 1987). Malgré le peu de connaissances relatives à la relation entre le régime hydrique et la transmission de la lumière (Zahner, 1968; Stadt *et al.*, 2005) on peut penser qu'une évapotranspiration moins élevée pourra permettre le maintien d'une surface foliaire plus élevée et ainsi contribuer à une interception de la lumière supérieure, comparativement à un site où l'évapotranspiration serait plus importante.

Dans le cadre de cette étude, nous avons caractérisé l'OC et l'allométrie de l'érable à sucre (*Acer saccharum* Marsh.) du bouleau jaune (*Betula alleghaniensis* Britton) et de la pruche du Canada (*Tsuga Canadensis* (L.) Carr.) pour les régions du Témiscamingue, de l'Ontario et de la péninsule supérieure du Michigan. Ces trois espèces coexistent dans le domaine de l'érablière à bouleau jaune, par contre le bouleau et la pruche occupent surtout les sites de bas de pente où l'apport en eau est important (Burns et Honkala, 1990). Le bouleau jaune est moyennement tolérant à

l'ombre et adopte une stratégie opportuniste en exhibant un taux de croissance élevé et en étant favorisé par les trouées (Burns et Honkala, 1990). Par contre, cela ne lui permet pas nécessairement d'utiliser l'espace de façon efficace avec sa couronne, comparativement à l'érable et à la pruche (Webster et Lorimer, 2003). Ces deux dernières espèces sont très tolérantes à l'ombre (Burns et Honkala, 1990).

Les objectifs principaux du premier chapitre étaient de comparer l'OC entre les espèces selon leur degré de tolérance à l'ombre, ainsi qu'entre les individus selon l'allométrie de leur cime (celle-ci étant reliée à leur statut social dans le peuplement), et entre les régions selon l'évapotranspiration.

Dans le deuxième chapitre, notre objectif était de déterminer dans quelle mesure l'OC et l'allométrie des arbres sont variables selon les régions et plus spécifiquement comment les paramètres du module de lumière de SORTIE variaient selon les régions, pour ces trois espèces.

CHAPITRE I

CROWN OPENNESS AS INFLUENCED BY TREE AND SITE CHARACTERISTICS

1.1 Résumé

L'ouverture de la couronne (OC) des arbres matures influence grandement la transmission de la lumière au travers de la canopée forestière. Pourtant, en modélisation elle est souvent considérée constante à l'intérieur d'une espèce peu importe les dimensions de l'individu ou sa provenance géographique. L'objectif de cette étude est de tester si l'OC est constante pour le bouleau jaune (*Betula alleghaniensis* Britton), l'érable à sucre (*Acer saccharum* Marsh.) et la pruche du Canada (*Tsuga canadensis* (L.) Carr.). Plus spécifiquement, l'influence des facteurs suivants : 1) le diamètre à hauteur de poitrine (DHP), 2) l'angle de transmission de la lumière par rapport au zénith, 3) l'allométrie de la couronne et 4) l'évapotranspiration sur la variation de l'OC a été testée. Les résultats suggèrent que l'OC diffère selon l'angle de transmission de la lumière, le DHP et du ratio diamètre de la couronne/DHP. Tandis que les arbres dominants peuvent intercepter la lumière latéralement (e.g., 45°) et verticalement (e.g., 0°), les petits arbres sont beaucoup plus efficaces pour intercepter la lumière verticale plutôt que latérale. Ceci suppose une distribution planophile du feuillage pour les petits arbres, ainsi qu'une tendance vers une distribution aléatoire de l'angle des feuilles au fil de l'ontogenèse. L'augmentation de l'évapotranspiration potentielle est associée à des couronnes plus ouvertes. Considérant le rôle important de l'OC au sein de la transmission de lumière en sous-bois, il serait nécessaire de mieux comprendre sa variabilité interspécifique, intraspécifique et régionale avant de l'intégrer dans les modèles de simulation de la dynamique forestière.

Mots clés : ouverture de la couronne, transmission de la lumière, allométrie, angle des feuilles, évapotranspiration potentielle.

1.2 Abstract

Crown openness (CO) of mature trees greatly influences light transmission within the forest canopy. Although in modeling, this variable is often considered constant within species while its regional variability is ignored. The objective of this study was to test how CO varies for yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). More specifically, the influence of 1) diameter at breast height (DBH), 2) angle of transmission from zenith, 3) crown allometry and 4) potential evapotranspiration (PET) on CO was tested. Results suggest that CO varies with DBH, angle of transmission, and crown width/DBH. While dominant trees can intercept light laterally (e.g., 45°) and vertically (e.g., 0°), smaller trees are only efficient at intercepting light vertically. This supposes a horizontal display of leaves for smaller trees with a tendency towards a random leaf angle distribution with ontogeny. Increasing PET is associated with more open crowns. Given its ecological importance, a better understanding of the variability of CO is needed before using the variable for modeling light predictions.

Key words: Crown openness, light transmission, allometry, leaf angle, potential evapotranspiration.

1.3 Introduction

Understory light regimes are fundamental to understand community dynamics of forests (that are not affected by large scale disturbances) because tree species regeneration largely depends on this resource to grow and reach the overstory. Light regimes are also important in forest management since by manipulating the canopy, one can favour some tree species over others (Lieffers *et al.*, 1999). Light availability in the understory is regulated by the climatic conditions, the position of the sun in the sky, the characteristics of the canopy cover and by the amount of gaps found at any time in a forest (Canham *et al.*, 1990; Lieffers *et al.*, 1999; Wirth *et al.*, 2001). Of all of these factors, the characteristics of individual crowns forming the canopy affect light transmission in the understory are probably those that have been the least studied (Canham *et al.*, 1994; Wirth *et al.*, 2001).

Different approaches have been used to model and predict light transmission through the canopy layer. Some models consider the canopy as a homogeneous and monolayered volume of foliage (Norman and Jarvis, 1975; Brown and Parker, 1994; Larsen and Kershaw, 1996). This representation of the canopy is appropriate for simulating light penetration in even-aged, monospecific stands that do not comprise gaps in the canopy, but cannot account for the variability of the light regime created by heterogonous canopies, such as found in forests of the temperate deciduous biome. A modeling approach where the forest canopy is represented as being composed of individual crowns can better allow the simulation of light transmission in forests with discontinuous canopies (e.g. see SORTIE in Pacala *et al.*, 1993; MIXLIGHT in Stadt and Lieffers, 2000, 2005; and tRAYci in Brunner, 1998; Gersonde *et al.*, 2004; Piboule *et al.*, 2005).

Light transmission is usually modeled following the Beer Law (Brown and Parker, 1994; Larsen and Kershaw, 1996; Lieffers *et al.*, 1999; Vose *et al.*, 1995; Stadt and Lieffers, 2000, 2005) where an extinction coefficient describes the ability of foliage to intercept light within a stand canopy or an individual crown. The Beer law assumes that the light absorbing elements (e.g. leaves) are randomly distributed within the canopy and that light is either transmitted or absorbed, i.e. that there is no light reflection and thus no beam enrichment. Since these assumptions are not representative of the spectral attributes of leaves, modeling light transmission by using the Beer law can introduce a bias in the prediction of transmitted light (Lieffers *et al.*, 1999; Stadt and Lieffers, 2000). The extinction coefficient usually comprises a measure of leaf area index (LAI) (Brown and Parker, 1994; Larsen and Kershaw, 1996) or leaf area density (LAD) (Brunner, 1998; Stadt and Lieffers, 2000, 2005), and is positively correlated to these variables. The coefficient can also include the path length, the distance covered by light rays within the crown, which varies with crown size (Pukkala *et al.*, 1993; Canham *et al.*, 1994).

Crown openness (CO), which represents the proportion of sky that can be seen through an individual crown (Astrup and Larson, 2006), can be equated to the light transmitted through a whole crown. Determining CO at the individual crown level (along with crown geometry information) can allow modeling light transmission at the stand level by combining the effect of individual tree crowns (that can be of different size and/or species) present in the neighborhood (e.g. with SORTIE, Pacala *et al.*, 1993). In other cases, LAD, also combined with crown geometry information, is used in individual-tree based models (see MIXLIGHT in Stadt and Lieffers, 2000, 2005; and tRAYci in Brunner, 1998; Gersonde *et al.*, 2004; Piboule *et al.*, 2005).

These spatially explicit models are promising from a management perspective because they can simulate complex stands, allowing to evaluate the consequences of

some of the new ecosystem-based silvicultural treatments proposed (Lieffers *et al.*, 1999; Messier *et al.*, 2003). However, such models often require much data and therefore have not been used or tested in many different environmental conditions. This is one of the main potential drawbacks of these models, i.e. that they have often been parameterized for only a few stands or regions (Lieffers *et al.*, 1999, Stadt and Lieffers, 2000; Sonohat *et al.*, 2004). Although a recent study by Astrup and Larson (2006) reported regional variability in CO for aspen and white spruce, we are usually unaware of how much variability there is for different parameters used in these models among regions with different biophysical conditions.

In the above-cited models, one of the most important parameter, e.i. the one describing the light extinction or transmission property of a tree crown, is generally defined using a species-specific value. For example, CO and light extinction coefficient have been related to species shade tolerance in previous studies (Horn, 1971; Canham *et al.*, 1994; Messier *et al.*, 1998; Lieffers *et al.*, 1999; Beaudet *et al.*, 2002, Kitajima *et al.*, 2005). The lower photosynthetic compensation point of shade tolerant species (Givnish, 1988) allows for more self-shading within the crown of shade tolerant species. Such species may have greater leaf area and/or longer crowns (Aiba and Kohyama, 1997; Canham *et al.*, 1994; Sterck *et al.*, 2001; Kitajima *et al.*, 2005) and therefore an increased light extinction ability and a reduced CO. Astrup and Larson (2006) reported that CO was independent of tree size (DBH) and angle of transmission, although only a limited range of angles was considered and a slight correlation between CO and DBH was found for white spruce. Not only in this case but also more generally, the fact that this ability to intercept light could also change with tree size or crown geometry is overlooked since light transmission (CO) or extinction parameters are considered constant among individuals, within species.

Regional variability in CO has been observed by Astrup and Larson (2006), but the effective environmental factor was not identified (the study failed to illustrate the effect of precipitation). Since potential evapotranspiration (PET) has been thought to be the environmental variable the most highly correlated with leaf area (Gholz, 1982) along with precipitation (Waring *et al.*, 1978; Grier and Running, 1977), the species ability to intercept light may increase with water availability. This has been suggested by Messier et al. (1998), but could not be confirmed by Sonohat et al. (2004) for coniferous stands in the temperate biome, nor by Stadt *et al.* (2005) for species of the boreal forest. According to Zahner (1968) and Stadt *et al.* (2005), there is a lack of information on this relationship.

The general objective of this study is to determine if and how (1) tree size and crown morphology and (2) variations in site conditions induced variations in CO among yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.) and eastern hemlock (*Tsuga Canadensis* (L.) Carr.) individuals of the temperate deciduous forest of northeast America. First, we will compare tree species according to their shade tolerance. Second, we will see if CO varies across regions differencing in annual PET. Third, we will investigate the effect of individual traits such as crown width and angle of transmission from the zenith on CO. We will then be able to determine if a constant CO can be used for a certain species independently of its size, crown morphology and biophysical environment.

1.4 Material and methods

1.4.1 Study area

All field measurements took place during the summer of 2004, between June 2nd and September 12th. The study sites were located in Témiscamingue (3 sites) in western Quebec, in the Haliburton forest (3 sites) in southern Ontario, and in the

Marquette (3 sites) and Menominee (2 sites) counties of the upper peninsula of Michigan (Figure 1.1, Table 1.1). All of these forests were uneven aged stands on mesic sites. They were dominated by sugar maple and had been recently harvested (selection cut within less than 2 years), so that tree crowns would not have had time to respond to the opening. For each site, three representative circular sampling plots of $400m^2$ located at least 100m apart, were established. At the center of these plots, position coordinates and altitude were determined with a Magellan *SportTrack* GPS, the altitude of the sites varied from 271m to 488m. Drainage ranged from moderate-slow to moderate-good and the slopes, measured in degrees with a clinometer, ranged from 0° to 15°. Basal area was measured with a diameter tape for individuals over 9 cm in diameter at breast height (DBH), and stumps were included in which case diameter was measured at base and DBH was inferred using allometric relationships (MRNFP, 2003) for the calculation of the plot pre-harvest basal area. Humus type and soil texture were determined according to the Canadian System of Soil Classification (1998). A soil sample of the B-horizon was taken in each plot at a depth of 20 to 25 cm (in the presence of two B-horizons, both were sampled). Cationic exchange capability (CEC) was obtained with an atomic absorption spectrophotometer (AAS) by using the barium chloride ($BaCl_2$) saturation technique. Acidity (pH) was measured in water with an electrode. Mean annual temperature and precipitation were obtained from monthly climate normals for the period between 1971-2000 for both countries (Stations *Chatham exp. farm 2* and *Escanaba* in Michigan: NOAA, 2002; stations *Algonquin park west* and *Barrage Témiscamink*: Environment Canada, 2004). Annual PET was calculated using 1) the monthly climate normals (air temperature and precipitation), 2) the water holding capacity of the soil corresponding to closed mature forest (Témiscamingue: fine sandy loam, other regions: silt loam), 3) conversion and computational tables, following the method of Thorntwaite and Mather (1957).Regions differed considerably from each other in their biophysical conditions, while sites within a region differed in a more

subtle manner (Table 1.1). Témiscamingue comprises the northernmost sites, although the regional PET was the second highest. This can be attributable to its shallow sandy soils (taken into account in the PET calculation), typically podzols (Brown, 1981). Témiscamingue represents a transitional forest between the deciduous at the south, maple dominated stands, and evergreen forests where balsam fir and spruce thrive, at the north. Sites sampled in Ontario (Haliburton forest) had the highest amount of precipitation and more fertile soils (higher CEC) of the brunisol order. Sites in the Marquette County were located less than 100 km from the south shore of lake Superior. The sites, where Black Cherry was common, seemed productive (high B.A.) despite an abnormally low CEC. The low CEC might be a consequence of the emission of heavy metals by the nearby coal plant in Marquette City, which cause the leaching of cations in the soil layer (Kimmins, 1987). Sites in Menominee had the highest PET, very fertile soils with a good proportion of clay, a high CEC and a less acidic pH. This indicates older soils where glaciers retreated earlier during the last ice age. Measures in the Menominee County were interrupted because of an early fall, therefore only two sites were completed.

A total of 451 yellow birch, 456 sugar maple and 423 hemlocks were measured (height, DBH and crown allometry), among which 159, 128 and 91 individual crowns were selected for evaluation of crown openness, for each species respectively. We sampled trees over 9 cm in DBH, with no sign of disease or senescence, which were not in proximity to roads or landings. At each site, we aimed at collecting data for trees from a range of DBH. In two regions (Témiscamingue and Marquette), eastern hemlock was not found in sufficient number at one of the sites so more individuals were sampled at another site of the same region to compensate.

1.4.2 Allometry measurements

Allometry measurements in the field included DBH, total tree height, height of crown base and crown width. For all individuals, DBH was measured with a diameter tape. Total tree height and height of crown base were measured with a hypsometer Haglöf Vertex III. Crown base was defined as the height of the lowest non-epicormic foliage, and crown depth was obtained by subtracting the height of crown base from total height. The diameter of the crown projection was measured orthogonally with a measuring tape, along north-south and east-west orientations. A clinometer was used to ensure that each measurement was taken vertically under the crown, at 90°. Crown radius was obtained by dividing the average diameter by two.

1.4.3 Crown openness measurements

Pictures of the crowns were taken with a Nikon Coolpix 950 digital camera with a definition of 2048 per 1536 pixels. Pictures were taken from four different angles of view (Figure 1.2) and the position of the camera was determined with a clinometer aimed at the top of the crown at 45°, 30°, 15° and 0°, so the height of the camera was taken into account. Only individuals that were not affected by the previous harvest and had isolated crowns were selected (i.e. the crown had to be viewed with the sky as a background). Pictures were taken in various conditions (blue or overcast skies) but were not taken during rain or wind events, which could alter leaf or branch position, and never encompassed the sun.

Crown openness values were obtained from the pictures following the methodology of Beaudet et al. (2002). The area on which CO was calculated consisted of a shape delimited within the crown, following the edge of the crown with a small buffer zone. Pictures were analyzed in Photoshop (v. 7.0) where the crown area was selected, crown elements (including branches) were transformed in black and sky in white, and the percentage of white pixels in the selected crown area was

calculated. The corresponding values of CO were then obtained and the mean of the values at the four angles was calculated in order to have a mean crown openness value per individual (the mean was calculated only for the individuals for which the pictures at the four angles were available, so the *n* of the analysis does not necessarily corresponds to the total of pictures divided by four).

1.4.4 Data analysis

Species differences in CO were tested with a one-way ANOVA followed by a post-hoc Tukey multiple comparison test. The influence of PET and species and the interaction between the two factors was tested in a two-way ANOVA. The effect of angle and DBH were simultaneously tested using a Generalized Linear Model (GLM) with repeated measures on CO with the DBH as a between subject factor and the effect of angle as a within subject factor. The same analysis was applied to angle and crown width/DBH (instead of DBH alone). The crown width/DBH ratio was chosen because this variable represents a display strategy at the whole tree level. The ratio illustrates how the tree invests in lateral crown display relatively to its DBH.

For all tests, homoscedasticity of the data was confirmed by plotting the residuals against the predicted values, while skewness and kurtosis of residuals were calculated to identify cases where a departure from normality would be present. Prior to the repeated measures analysis, residuals of CO values at 0°, 15°, 30° and 45° were pooled to test normality, in addition to the previous test of normality on residuals of the variance analysis of mean CO and DBH and crown width/DBH ratio. In any cases did data needed to be transformed, but two outliers were deleted. For the repeated measures analysis, assumption of sphericity of the covariance matrix is met when epsilon values (Greenhouse-Geisser, G-G and Huynh-Feldt, H-F) are close to one (higher than 0.75). We relied on the H-F's corrected probability if the H-F epsilon

value was > 0.75, and on the more conservative G-G's corrected probability when the H-F value was < 0.75 (Quinn and Keough, 2003). All analyses were performed using SYSTAT (v. 10.0).

1.5 Results

1.5.1 Interspecific differences in crown openness

Mean CO differed among species (Table 1.2). Yellow birch had the highest mean CO (15.1 ± 6.1 %, mean ± SD) while sugar maple (10.5 ± 4.4 %) and eastern hemlock (11.0 ± 4.5 %) had similar mean CO values (post-hoc Tukey test, results not shown).

1.5.2 Effect of potential evapotranspiration on crown openness

Crown openness (CO) clearly increases with increasing regional PET (Figure 1.3; Table 1.3). The effects of species is not significant for this analysis because of the low *n*, but yellow birch has a higher mean CO than the other 2 species. The non-significant interaction indicates that all species CO respond in the same direction to an increase in PET.

1.5.3 Effect of angle and DBH on crown openness

The repeated measures analysis confirms the strong effect of DBH on CO as a source of variation between subjects (Table 1.4) for yellow birch and sugar maple. The analysis also reveals that there is a significant interaction between angle and DBH (Table 1.3) for yellow birch and sugar maple, indicating that the angle effect on CO varies with tree DBH and meaning that the two effects cannot be interpreted separately. In Figure 1.4, values of CO grouped by the angle from zenith are plotted against DBH. CO varies depending on angle and two different trends can be detected.

First, the CO tends to vary less as a function of DBH at 0° from zenith. Secondly, the variability of CO as a function of the angle of transmission is greater for trees with smaller DBH compare to larger trees. For eastern hemlock, only the angle has a significant effect on CO (Table 1.4).

1.5.4 Effect of angle and crown width/DBH on crown openness

Crown openness tends to increase with increasing crown width/DBH ratio for yellow birch and sugar maple, but this effect is apparent mainly for the two highest angles (Figure 1.5). This is clearly illustrated in Table 1.5 by the significant interaction between angle and crown width/DBH for yellow birch and sugar maple. For eastern hemlock, only the angle has a significant effect on (Table 1.5).

1.6 Discussion

1.6.1 Interspecific differences in crown openness

Crown openness values calculated in this study are comparable to values obtained in other studies using a similar method (Canham *et al.*, 1999; Beaudet *et al.*, 2002; Poulin *et al.*, 2004; Astrup and Larson, 2006), which are usually between 10 and 20% for trees species of northeastern America. Our results also confirmed that more shade intolerant species (such as yellow birch) tend to have higher CO values than shade tolerant species, such as sugar maple (Messier and Bellefleur, 1988; Canham *et al.*, 1994; Beaudet *et al.*, 2002). If compared solely with other results for the same species, our results agree with Horn (1971), but differ slightly from those of Canham et al. (1994), who found that eastern hemlock was casting more shade than sugar maple. In this study, we did not detect any significant difference between those two species. These discrepancies could be attributed to differences in methodology. In Canham et al. (1994), CO was derived from hemispherical photographs of the

whole forest canopy, and so they included stand-level canopy features in addition to individual tree crown characteristics. Stand–level canopy openness of eastern hemlock might therefore be lower than for sugar maple, while the two species might not differ in terms of crown-level openness.

1.6.2 Effect of potential evapotranspiration on crown openness

Our results on the effect of regional PET on CO agree with the general assumption that the quantity of foliage decreases with decreasing water availability (Zahner, 1968; Jose and Gillespie, 1996). While the effect of precipitation could not be identified in the regional variability of CO found by Atsrup and Larson (2006), our result suggest that regional PET contribute to changes in CO, amongst other environmental factors. This has been hypothesized before by Messier et al. (1998) to explain the lower general light transmission of stands of *Populus tremuloides* in moist eastern Canada compared to stands in dry western Canada.

1.6.3 Effect of angle of transmission and DBH or crown width/DBH on crown openness

The variation of CO with both DBH and angle of transmission (Table 1.3, Figure 1.3) for sugar maple and yellow birch does not agree with the results of Astrup and Larson (2006) for white spruce and aspen. In the latter study, the angle did not affect CO. However, the range of angles of transmission in Astrup and Larson (2006) considered was limited (mostly between 0° and 15° from zenith) compared to ours (0° to 45° from zenith), mainly because their method consisted of taking pictures with a hemispherical lens aiming at zenith. As for DBH, the effect found in Astrup and Larson (2006) was limited to a weak one for white spruce, while a significant effect was found for both deciduous species in this study. Both angle of transmission and DBH influence variation in CO with a significant interaction (Table 1.3, Figure 1.4)

although crown allometry should not be ignored either as an effect can be observed too.

The ratio of crown width/DBH can be used as a mean to describe the degree of lateral crown display of a tree in relation to its DBH. The ratio is negatively correlated to individual tree height (results not shown) and can be considered as an index of the social status of a tree in a forest. Trees with a high ratio usually have more horizontal crowns such as found among individuals that occupy the understory (Horn 1971; King, 1991). For hemlock, the ratio is generally lower than for deciduous species, which is rather typical for gymnosperm trees compared to angiosperms (King 1991, Oliver and Larsen 1996; Piboule *et al.*, 2005). For hemlock, crown width/DBH did not influence CO, but the angle of measurement showed a rather strong effect on CO, with an increase of CO at higher angles (30°, 45°). For sugar maple and yellow birch, the crown width/DBH ratio interacted with the angle of measurement to explain much of the variation observed in CO (Table 1.4, Figure 1.5). This interaction indicates that for trees with a high ratio (presumably the smaller ones growing below the dominant trees), crown openness shows greater variation as a function of the angle of transmission, as would be expected for trees with a more horizontal leaf display.

Most models assume that crown's light transmission properties do not vary with the direction of the incoming light. However, our results show a strong effect the angle of transmission for the two broadleaved species. Results show (Figure 1.4) that there is clearly an increase CO with the angle from zenith, at least among smaller trees and among those with a high crown width/DBH ratio. There are many possible explanations for this interaction between the angle of transmission and tree size effect.

First, the larger the crown, the higher probability that leaves would intercept light no matter the angle of measurements. Second, if smaller trees are suppressed, they receive less lateral light (Horn, 1971) and may have more horizontal leaves in general than the dominant trees. This "horizontal efficiency" as expressed by Falster and Westoby (2003) is typically employed by smaller or suppressed trees in the understory (Givnish, 1988; Horn, 1971, Niinemets *et al.*, 2005) to maximize their light interception and cast shade on competitors. As crown width/DBH increases, the leaf angle distribution changes and CO augments with higher angles (30°, 45°). This suggests that the dominant trees are much more efficient at intercepting light coming from all directions than the suppressed and smaller trees. It also shows that CO is not a constant parameter within a tree species, but can vary either through ontogeny or due to shading. As individuals grow in height, they experience an increase in light availability from many directions (Aiba and Kohyama, 1997; Osada *et al.*, 2004; Sterck and Bongers, 2005). As a result, during ontogeny, leaf and branch display is subject to change and this can ultimately translate in the development of orthotropic branches (Horn, 1971; King, 1991; King and Maindonald, 1999; Niinemets *et al.*, 2005) where leaves with a steeper angle can maximize light interception at low angles while minimizing respiration cost and avoiding photoinhibition (Givnish, 1988; Falster and Westoby, 2003). Given that a random leaf angle distribution allows for optimal light interception efficiency when the light source is multidirectional (Barclay, 2001; Sinoquet *et al.*, 2005), our results suggest that the leaf angle distribution is preferentially horizontal among smaller individuals (hence the higher CO when the crowns are viewed from the side) and becomes increasingly random with increasing tree size (since crown openness does not vary as much with angle of transmission among larger trees). This confirms that with an increase of light from the side, trees can modify their leaf angle distribution enabling them to fully exploit this resource (Aiba and Kohyama, 1997; Sterck *et al.*, 2001).

The increase of CO with the crown width/DBH ratio can also be explained by the uneven distribution of foliage within the canopy strata and within the crowns. Trees with a high ratio that typically occupy the understory or the sub-canopy could have a reduced amount of LAD since most of the foliage is usually concentrated on the top layer of the canopy (Brown and Parker, 1994; Vose *et al.*, 1995; Kitajima *et al.*, 2005), and a sparse display of foliage would lead to a higher CO.It is believed that CO varies depending on the path length, as hypothesised by Astrup and Larson (2006). This was not proven in this study (results not shown) possibly because of a heterogeneous distribution of leaves within the crown. Horn (1971) illustrated this phenomenon by showing that mature hardwood trees usually have a hollow at the centre of their crowns, the effect being greater for shade intolerant trees (Canham *et al.*, 1994; Sterck *et al.*, 2001). In a modeling experiment, Canham et al. (1994) also pointed out that accounting for this type of leaf distribution in modelling light transmission increased the accuracy of the predictions, as opposed to considering the crown volume homogenous (as in a path length model).

1.7 Conclusion

This study confirmed that CO is greater in shade intolerant compared to more shade tolerant species. However, it showed that this parameter is not constant within a species and that it tends to vary according to the biophysical conditions as well as with the angle of transmission and the size (DBH) and crown shape of trees. The relative differences among tree species appear to hold. Although we have shown CO to vary among species, tree size or tree position within the canopy, in relation to the angle of transmission and among climatic regions, we do not know if such differences are ecologically significant. For example, the higher CO attributed to suppressed trees might not be contributing much to the overall dynamic of light transmission in forests. Furthermore, Beaudet et al. (2002) and Canham et al. (1994) have shown that changes in CO have relatively less impact on light transmission than changes in

crown geometry variables. The same phenomenon was observed with the tRAYci model when changes in LAD did not affect light predictions significantly (Gersonde *et al.*, 2004; Piboule *et al.*, 2005). Further research is needed to better assess the potential ecological impacts of variations of CO.

1.8 Acknowledgements

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1.9 Tables and Figures

1.9.1 Tables

Table 1.1 Summary of regional and site characteristics (average values of 3 plots).

Region	Mean annual temperature (C°)	Annual evapotrans-piration (mm)	Sites coordinates	Mean CEC	pH	Soil texture	Humus type	Mean B. A. before harvest (m^2/ha)*	Mean density (trees/ha)*	Stand species composition**
Témiscamingue			46° 40' N, 78° 30' E.	2.00	4.43	loam	moder	23.3	525	SM, YB, EH.
	4.,4	556.3	46° 37' N, 78° 08' E.	3.36	4.91	sandy loam	moder	16.3	525	SM, EH.
			46° 24' N, 78° 15' E.	2.99	5.03	sandy loam	moder	23.8	450	SM, YB, AB.
Haliburton			45° 14' N, 78° 37' E.	3.30	4.93	sandy loam	mor-moder	26.0	550	SM, EH, AB, YB.
	4,9	530.8	45° 14' N, 78° 37' E.	3.71	5.04	sandy loam	moder	24.4	492	SM, YB, EH.
			45° 21' N, 78° 32' E.	2.24	4.26	loam	moder	22.6	608	SM, BF, YB, EH.
Marquette			46° 20' N, 87° 19' E.	1.04	4.50	sandy loam	moder	32.5	525	SM, BC, YB, EH.
	3,9	537.6	46° 20' N, 87° 20' E.	0.66	4.26	sandy loam	moder	40.8	500	SM, YB.
			46° 20' N, 87° 17' E.	2.75	4.45	sandy loam	moder	38.5	617	SM, BC.
Menominee	5,5	559.8	45° 45' N, 87° 28' E.	6.54	5.91	clay loam	mull	27.9	667	SM, EH
			45° 45' N, 87° 35' E.	10.56	6,32	clay loam	mull	46.6	517	SM, YB, BF.

*for trees over 9 cm in DBH and including stumps in harvested plots.

** listed for each site in decreasing order of dominance: SM: sugar maple, YB: yellow birch, EH: eastern hemlock, AB: American beech, BF: balsam fir, BC: black cherry.

Table 1.2 Summary of ANOVA to test the effect of species (categorical factor) on mean crown openness.

Source	**df**	**Mean-Square**	***F*-ratio**	***P***
Species	2	771.146	28.442	<0.001
Error	310	27.113		

Table 1.3 Summary of two-way ANOVA where the effect of species and potential evapotranspiration and their interaction on crown openness is tested.

Source	**df**	**Mean-Square**	***F*-ratio**	***P***
Species	2	2.4	0.6	0.581
PET	1	29.1	7.3	0.036
Species X PET	2	2.7	0.7	0.546
Error	6	4.0		

Table 1.4 Results of the repeated measures analysis where crown openness is the dependent variable, DBH is a between subject factor and angle is a within subject factor and the interaction between both factor is tested. Analysis was done separately for each species.

Species	Sources	SS	df	MS	F	P	H-F corrected P	G-G corrected P
Yellow birch	Between subject							
	DBH	602.2	1	602.1	4.185	0.043	---	---
	Error	19422.8	135	143.9				
	Within subject							
	Angle	1558.9	3	519.6	28.418	<0.001	<0.001	<0.001
	Angle x DBH	533.9	3	178.0	9.734	<0.001	<0.001	<0.001
	Error	7405.3	405	18.3				
	G-G epsilon: 0.821							
	H-F epsilon: 0.844							
Sugar maple	Between subject							
	DBH	768.9	1	768.9	10.906	0.001	---	---
	Error	7543.0	107	70.5				
	Within subject							
	Angle	881.3	3	293.8	26.921	<0.001	<0.001	<0.001
	Angle x DBH	190.3	3	63.4	5.818	0.001	0.018	0.017
	Error	3502.7	321	10.9				
	G-G epsilon: 0.732							
	H-F epsilon: 0.755							
Eastern hemlock	Between subject							
	DBH	177.9	1	177.9	2.299	0.134		
	Error	5107.1	66	77.38				
	Within subject							
	Angle	443.4	3	147.8	8.25	<0.001	<0.001	<0.001
	Angle x DBH	70.8	3	23.6	1.317	0.270	0.271	0.270
	Error	3547.0	198	17.9				
	G-G epsilon: 0.949							
	H-F epsilon: 1.000							

Table 1.5 Results of the repeated measures analysis where crown openness is the dependent variable, crown width/DBH is a between subject factor and angle is a within subject factor and the interaction between both factor is tested. Analysis was done separately for each species.

Species	Sources	SS	df	MS	F	P	H-F corrected P	G-G corrected P
Yellow birch	Between subject							
	Crown width/DBH	712.5	1	712.5	4.980	0.027	---	---
	Error	19312.5	135	143.1				
	Within subject							
	Angle	185.7	3	61.9	3.508	0.015	0.022	0.021
	Angle x Crown width/DBH	792.9	3	264.3	14.979	<0.001	<0.001	<0.001
	Error	7146.3	405	17.6				
	G-G epsilon: 0.832							
	H-F epsilon: 0.855							
Sugar maple	Between subject							
	Crown width/DBH	1030.1	1	1030.1	15.137	0.000	---	---
	Error	7281.7	107	68.1				
	Within subject							
	Angle	0.9	3	0.3	0.027	0.994	0.981	0.983
	Angle x Crown width/DBH	234.6	3	78.2	7.259	<0.001	0.001	<0.001
	Error	3458.4	321	10.8				
	G-G epsilon: 0.737							
	H-F epsilon: 0.760							
Eastern hemlock	Between subject							
	Crown width/DBH	11.4	1	11.4	0.143	0.707		
	Error	5273.6	66	79.9				
	Within subject							
	Angle	217.1	3	72.4	3.976	0.009	0.010	0.009
	Angle x Crown width/DBH	13.736	3	4.6	0.252	0.860	0.849	0.860
	Error	3604.0	198	18.2				
	G-G epsilon: 0.941							
	H-F epsilon: 1.000							

1.9.2 Legends for figures

Figure 1.1 Map of study area with location of sampling sites in 1) Témiscamingue, 2) Ontario, 3) Marquette county and 4) Menominee county.

Figure 1.2 Measures of variables for each tree include DBH and a) crown width; b) total tree height; c) crown depth. Pictures were taken at 45°, 30°, 15° and 0° from zenith (locations represented by the black dots indicated on the d line).

Figure 1.3 Mean regional crown openness as a function of potential evapotranspiration (mm/year) for yellow birch, sugar maple, eastern hemlock .

Figure 1.4 CO as a function of DBH grouped by angle of transmission for A) yellow birch, B) sugar maple and C) eastern hemlock. Total sample size (all angles included) is 604 for yellow birch, 488 for sugar maple and 335 for eastern hemlock; data from all sites are included.

Figure 1.5 CO as a function of crown width/DBH grouped by angle of transmission for A) yellow birch, B) sugar maple and C) eastern hemlock. Total sample size (all angles included) is 604 for yellow birch, 488 for sugar maple and 335 for eastern hemlock; data from all sites are included.

1.9.3 Figures

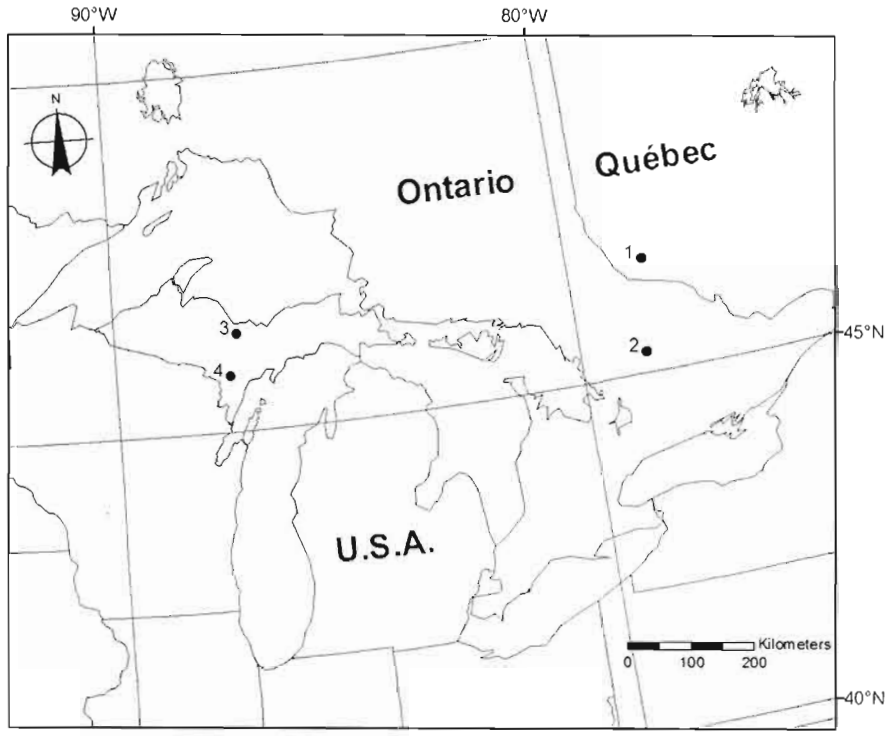

Figure 1.1

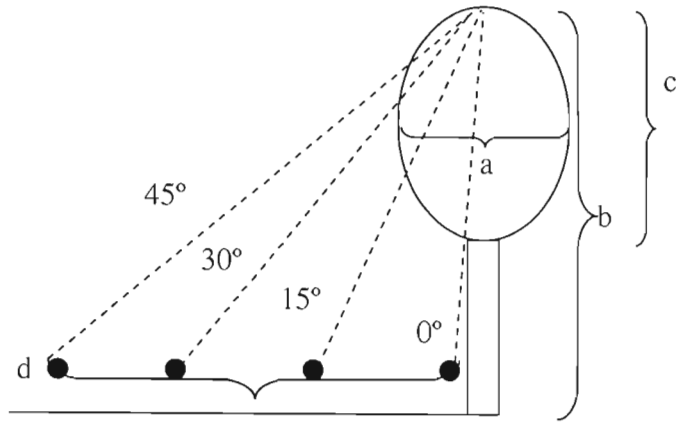

Figure 1.2

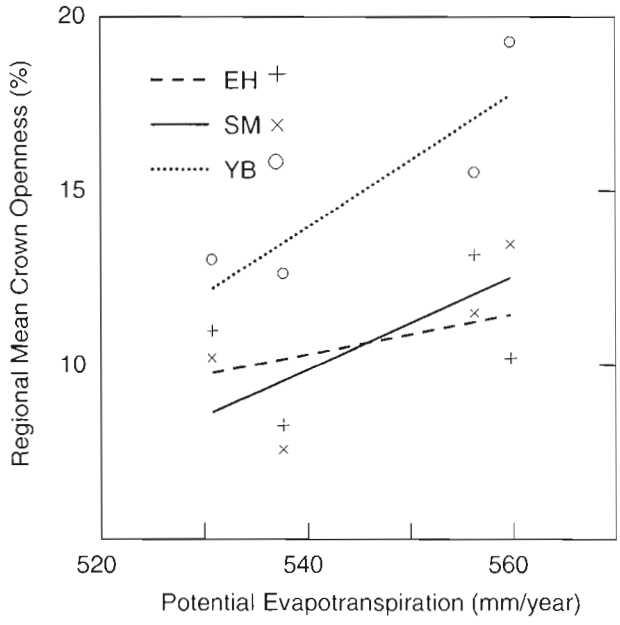
20
15
10
EH +
SM ×
YB ○
Regional Mean Crown Openness (%)
520
540
560
Potential Evapotranspiration (mm/year)

Figure 1.3

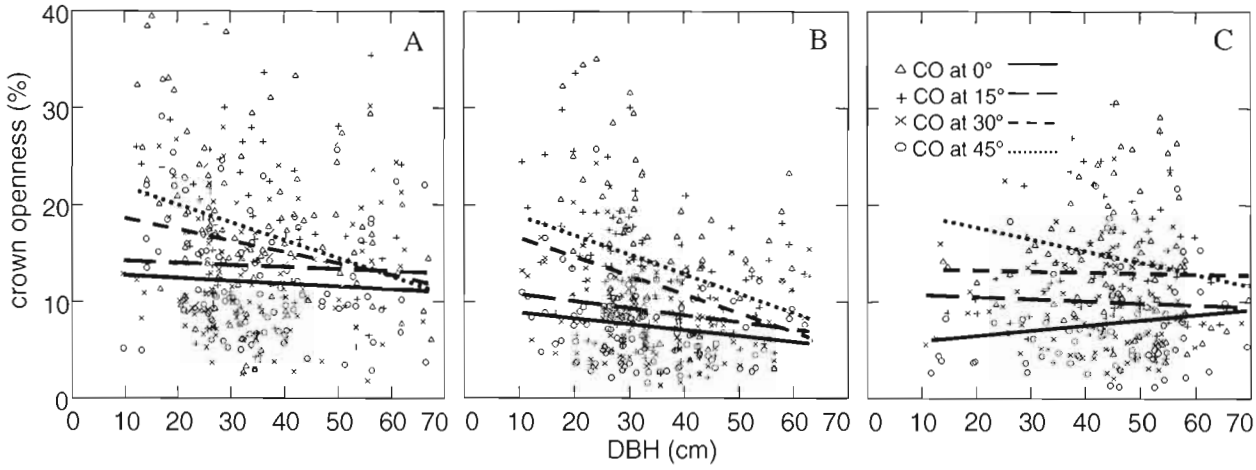
A
B
C
crown openness (%)
DBH (cm)
△ CO at 0°
+ CO at 15°
× CO at 30°
○ CO at 45°
0
10
20
30
40
50
60
70

Figure 1.4

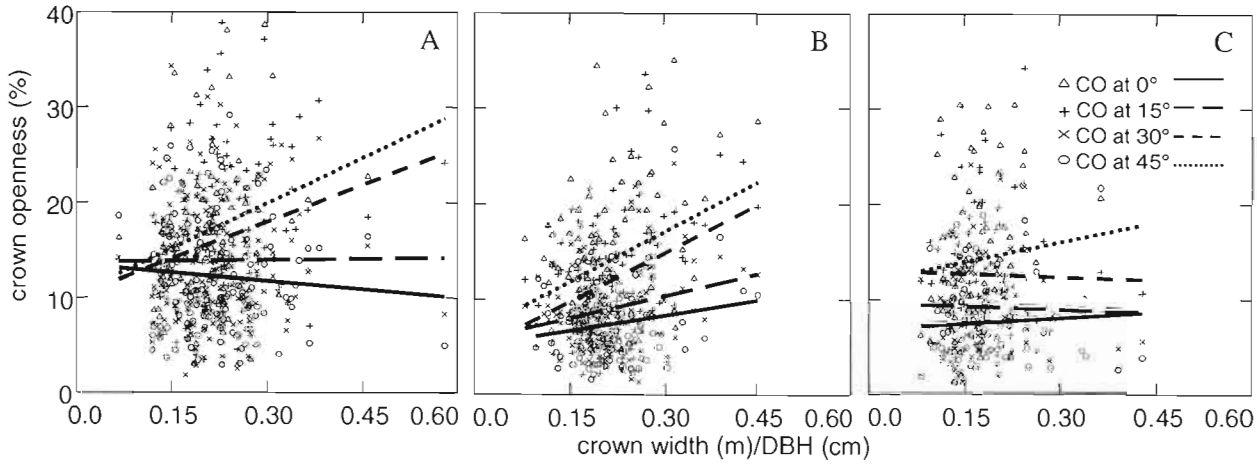
A
B
C
crown openness (%)
crown width (m)/DBH (cm)
CO at 0°
CO at 15°
CO at 30°
CO at 45°
0
10
20
30
40
0.0
0.15
0.30
0.45
0.60

Figure 1.5

CHAPITRE II

REGIONAL VARIABILITY OF CROWN OPENNESS AND ALLOMETRY FOR YELLOW BIRCH, SUGAR MAPLE AND EASTERN HEMLOCK: IMPLICATIONS FOR THE PARAMETERIZATION OF THE SORTIE LIGHT MODEL.

2.1 Résumé

Nous avons paramétrisé le module de lumière du modèle SORTIE, un modèle dynamique de croissance forestière, pour le bouleau jaune (*Betula alleghaniensis* Britton), l'érable à sucre (*Acer saccharum* Marsh.) et la pruche du Canada (*Tsuga canadensis* (L.) Carr.). Les données ont été récoltées dans plusieurs régions (Témiscamingue, Ontario et Michigan) pour tester la variabilité des paramètres au travers des sites. L'échantillon total consistait en 451 bouleaux jaunes, 456 érables à sucre et 423 pruches du Canada pour les mesures allométriques, parmi lesquels un sous-échantillon a été sélectionné pour la mesure de l'ouverture de la couronne. Les différences des paramètres allométriques entre les espèces sont plus marquées que celle entre les sites. Ces dernières peuvent être attribuées aux conditions biophysiques des sites et au niveau des caractéristiques de peuplement (e.g. compétition, historique du site). L'ouverture de la couronne varie selon les espèces et les régions, mais les différences entre espèces à l'intérieur des régions ne sont pas constantes. Une analyse de sensibilité du modèle devra être conduite à l'aide de simulations afin de déterminer si les variations observées dans les paramètres ont un effet dans les prédictions de lumière en sous-couvert.

Mots clés: SORTIE, ouverture de la couronne, paramètres allométriques, variabilité régionale

2.2 Abstract

A forest dynamic growth model, SORTIE, precisely its light submodel, was parameterized for yellow birch *(Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). Necessary data was collected in various regions (Témiscamingue, Ontario and Michigan) to test parameter's variability across sites of the temperate deciduous biome. Total sample size was 451 yellow birches, 456 sugar maples and 423 eastern hemlocks for allometric measurements, among which a subsample of individuals was selected for crown openness measurement. For allometric parameters, differentiation between species is stronger than between regions. The latter can be explained by different biophysical conditions, along with stand characteristics (e.g. competition and site history). Crown openness varies according to species and region, but species differences within sites are not consistent. A sensitivity analysis of the model should be conducted, where the effect of the parameter's variability on the light predictions can be assessed.

Key words: SORTIE, crown openness, allometric parameters, regional variability.

2.3 Introduction

SORTIE is a forest dynamic model that was originally developed and parameterized for the transitional deciduous forests of northeastern United States (Pacala *et al.*, 1993; Pacala *et al.*, 1996). It has also been parameterized for cedar-hemlock forests in British Columbia (Canham *et al.*, 1999), and other ongoing parameterization initiatives include those for the boreal forest of Abitibi in Québec (Poulin *et al.*, 2004), the deciduous forest of southern Québec (Beaudet *et al.*, 2002), temperate forests of New Zealand and tropical forests of Puerto-Rico.

SORTIE is an individual-based, spatially explicit model, that comprises four main submodels (growth, light, regeneration, mortality) which all need to be parameterized for simulations. In SORTIE, each individual tree has x and y coordinates. Predictions of light transmission (i.e Gap Light Index (GLI)), are also spatially explicit so that a detailed output map can be obtained.

The light submodel is pivotal for the functioning of the model because calculations of sapling growth are based on the output of this specific submodel, and sapling mortality is based on sapling growth. GLI values can potentially be calculated for any location in the understory and depend on the presence, location, species identity and DBH of neighboring trees. The species identity will determine which allometry and crown openness (CO) each tree will have. Species-specific parameters of allometric relationships determine height and crown shape based on the DBH of the individual, while the species-specific CO parameter determines the ability of the species to transmit light.

It is fundamental to understand how the parameters needed for the parameterization of the light submodel vary depending on where the data is collected. A recent study by Astrup and Larson (2006) showed that CO values could vary between regions for aspen and white spruce, although the model's sensitivity to such variations was not tested. It is unknown how the species-specific parameters will vary among regions and whether the results of simulations can be generalized across a region or a biome for yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.) and eastern hemlock (*Tsuga Canadensis* (L.) Carr.), which are ecologically important and merchantable species of the temperate deciduous biome. Therefore, our objectives in this study were 1) to parameterize the SORTIE light submodel for yellow birch, sugar maple, and eastern hemlock from different sites across the temperate deciduous biome, and 2) to evaluate the differences between parameters obtained from different regions.

2.4 Material and methods

2.4.1 Parameterization of the light submodel

The light submodel requires the parameterization of three allometric equations and a canopy openness coefficient in order to process the calculations of the Gap Light Index (GLI).

Parameters of allometric relationships for mature trees are obtained by fitting the data to the following equations. Equation 1 is used to predict height from diameter at breast height (DBH):

[eq.1] $H=1.35+(H1-1.35)*[1-e^{(-1*DBH*B)}]$

where H represents total tree height in m, DBH is in cm and H1 and B are the parameters to estimate. In this relationship, H reaches an asymptote determined by H1 and B represents the steepness of the slope. Equation 2 illustrates how crown radius (m) is predicted from DBH using a power function, where C1 and CREXP are the parameters to estimate.

[eq.2] Crown radius= $C1*DBH^{CREXP}$

Equation 3 illustrates how crown depth (m) can be predicted from tree height (H) again using a power function, where C2 and CDEXP are the parameters to estimate.

[eq.3] Crown depth=$C2*H^{CDEXP}$

Species-specific mean crown openness (CO) values were obtained directly from crown pictures taken in the field, as explained in the section below.

2.4.2 Study sites

All field measurements took place during the summer of 2004, between June 2nd and September 12th. The study sites were located in Témiscamingue (3 sites) in western Quebec, in the Haliburton forest (3 sites) in southern Ontario, and in the Marquette (3 sites) and Menominee (2 sites) counties of the upper peninsula of Michigan (Table 2.1). All of these forests were uneven aged stands on mesic sites. They were dominated by sugar maple and had been recently harvested (selection cut

within less than 2 years), so that tree crowns would not have had time to respond to the opening. For each site, three representative circular sampling plots of $400m^2$ located at least 100m apart, were established. At the center of these plots, position coordinates and altitude were determined with a Magellan *SportTrack* GPS, the altitude of the sites varied from 271m to 488m. Drainage ranged from moderate-slow to moderate good and the slopes, measured in degrees with a clinometer ranged from 0 to 15°. Basal area was measured with a diameter tape for individuals over 9 cm in diameter at breast height (DBH), and stumps were included in which case diameter was measured at base and DBH was inferred using allometric relationships (MRNFP, 2003) for the calculation of the plot pre-harvest basal area: humus type and soil texture were determined according to the Canadian System of Soil Classification (1998). A soil sample of the B-horizon was taken in each plot at a depth of 20 to 25 cm (in the presence of two B-horizons, both were sampled). Cationic exchange capability (CEC) was obtained with an atomic absorption spectrophotometer (AAS) by using the barium chloride ($BaCl_2$) saturation technique. Acidity (pH) was measured in water with an electrode. Mean annual temperature and precipitation were obtained from monthly climate normals for the period between 1971-2000 for both countries (Stations *Chatham exp. farm 2* and *Escanaba* in Michigan: NOAA, 2002; stations *Algonquin park west* and *Barrage Témiscamingue*: Environment Canada, 2004). Annual PET was calculated using 1) the monthly climate normals (air temperature and precipitation), 2) the water holding capacity of the soil corresponding to closed mature forest (Témiscamingue: fine sandy loam, other regions: silt loam), 3) conversion and computational tables, following the method of Thorntwaite and Mather (1957).

Regions differed considerably from each other, while sites within a region differed in a more subtle manner (Table 2.1). Témiscamingue comprises the northernmost sites, although the regional PET was the second highest. This can be attributable to its shallow sandy soils (taken into account in the PET calculation), typically podzols (Brown, 1981). Témiscamingue represents a transitional forest between the deciduous forest in the south (maple dominated stands) and evergreen forests where balsam fir and spruce thrive, in the north. American beech was present only in the southernmost site. Sites sampled in Ontario (Haliburton forest) had the highest amount of precipitation and more fertile soils (higher CEC) of the brunisol order. Sites in the Marquette County were located less than 100 km from the south shore of lake Superior. The sites, where black cherry was common, seemed productive (high B.A.) despite an abnormally low CEC. The low CEC might be a consequence of the emission of heavy metals by the nearby coal plant in Marquette City, which cause the leaching of cations in the soil layer (Kimmins, 1987). Sites in Menominee had the highest PET, very fertile soils with a good proportion of clay, a high CEC and less acidic pH. This indicates older soils where glaciers retreated earlier during the last ice age. Measures in the Menominee County were interrupted because of an early fall, therefore only two sites were completed.

A total of 451 yellow birch, 456 sugar maple and 423 hemlocks were measured (height, DBH and crown allometry), among which respectively 159, 128 and 91 individual crowns were selected (Table 2.2) for determination of crown openness values (see below). Individual trees were often selected along the skid trails to facilitate measurements, but trees in proximity to roads or landings were not selected. The size of the area sampled at each site depended on the ease with which suitable individuals, with no sign of disease or senescence, were found. At each site,

we aimed at sampling approximately 30 individuals, as much as possible equally distributed among DBH classes. In two regions (Témiscamingue and Marquette), eastern hemlock was not found in sufficient number at one of the sites so more individuals were sampled at another site of the same region to compensate.

2.4.3 Allometric measurements

For all individuals, DBH was measured at 1.3 m above ground with a diameter tape. Total tree height was measured with a hypsometer Haglöf Vertex III. The base of the crown was defined as the height at which was the lowest nonepicormic foliage. Crown depth was obtained by subtracting height of crown base from total height. Crown diameter was measured orthogonally with a measuring tape, according to one north-south and one east-west transect with the use of a clinometer to ensure the measurement was taken vertically under the crown, at 90°. Crown radius was obtained by dividing the average diameter by two.

2.4.4 Crown openness

Pictures of the crowns were taken on a subsample of the trees selected for allometric measurements. Pictures were taken with a Nikon Coolpix 950 digital camera at four angles of observation. The position of the camera was determined with a clinometer aimed at the top of the crown at 45°, 30°, 15° and 0°, so the height of the camera was taken into account (Figure 2.1). This range of angle was chosen because it precisely corresponds to the range of light penetration through crowns in SORTIE light submodel. Only individuals with isolated crowns were selected to facilitate picture treatment. Pictures were taken in various conditions (blue or overcast skies)

but never encompassed the sun, and were not taken during rain or wind events, which could alter leaf or branch position.

Crown openness values were obtained from the pictures following the methodology of Beaudet et al. (2002). Pictures were analyzed in Photoshop (v. 7.0). The crown area was delimited using the Marquee tool. The image was thresholded so that crown elements (including branches) would be transformed in black, and sky in white. The percentage of white pixels in the crown area was then calculated (Figure 2.2). The corresponding values of crown openness were then obtained and the mean of the values at the four angles was calculated in order to have a mean CO value per individual.

2.4.5 Statistical analyses

Parameter values for the three allometric equations were determined by species and region (data from multiple sites, in each region, were pooled) using non-linear regression (NON LIN) in Systat (v.10.0). Equations (1, 2 and 3) were used and the following corresponding starting values were specified in Systat (first and second parameter value, in each of the three equations: 25, 0.05; 0.5, 0.5; 0.6, 0.8). Residuals were saved. Scatterplot of standardized residual vs. estimated values were examined to ensure homoscedacity, and skewness and kurtosis of the residuals were calculated to identify cases were a departure from normality would be present. Outliers were deleted. Confidence intervals (95%, C.I.) are reported. Parameter values with non-overlapping C.I. are considered to be significantly different at $P<0.05$.

To evaluate how CO varied as a function of regions and all species, an ANOVA combining species and regions as factors (and their interaction) was

performed. In the case of a significant interaction between the two factors, meaning that differences between species vary according to region one-way ANOVA was performed, separately for each region to test the effect of species. Scatterplot of standardized residual vs. estimated values were examined to ensure homoscedacity, and skewness and kurtosis of the residuals were calculated to identify cases were a departure from normality would be present. When the species effect was significant, a post-hoc Tukey test was performed to indicate which species are different from one another.

2.5 Results

2.5.1 Tree allometry

Values of the parameters allowing to predict height from DBH (eq. 1) are summarized in Table 2.3. Species differed in the height vs. DBH relationship, as represented in Figure 2.3. Yellow birch generally has a lower asymptotic height than the other species. Yellow birch shows considerable variability (among individuals) leading to generally lower r^2 values than the other species. Values of the maximum height parameter (H1) did not differ among regions for yellow birch, in part due to the wide confidence intervals. The slope (parameter B) however showed some differences among regions (Table 1.3). Sugar maple had a higher asymptotic height compared to yellow birch. The H1 parameter is different for Témiscamingue compare to Ontario and Menominee, while B was only different for Marquette. The eastern hemlock height-DBH relationship seems variable but the confidence intervals of the parameters are overlapping in all cases. Sugar maple and eastern hemlock individuals are taller at sites with a high PET (Table 2.1), but because of higher slope values, sugar maple reaches greater heights at smaller DBH.

Parameters obtained for eq. 2 are found in Table 2.4. Values of both parameters were not distinct among regions, although different tendencies can be observed for this relationship (Figure 2.4). The two most tolerant species exhibit wider crowns for smaller size (Figure 2.4) represented by C1 values that are generally higher (Table 2.4), compared to yellow birch. The highest curve for yellow birch represents values for the Menominee County, which is the most fertile and dry region. For sugar maple, figure 2.4 shows that crown radius is lowest in Témiscamingue, the northernmost region. In all cases, i.e. all species and regions, the exponent was significantly smaller than one, indicating that the relationship between crown radius and DBH is not linear.

Parameters of the last equation (eq. 3) predicting crown depth from total height are found in Table 2.5. Differences between the two deciduous species and the conifer are observed with the CDEXP exponent being not different from 1 for hemlock and being generally different from 1 for the other two species. This indicates a linear relationship for the hemlock, which means that tall trees have proportionally longer crowns.

2.5.2 Crown openness

Mean CO values (average of four angles) varied per species and region with a significant interaction between the two factors (Table 2.6), meaning that the effect of these factors cannot be interpreted separately. A one-way ANOVA shows that CO varies among species within each region, with the exception of Ontario (Table 2.8). The highest CO values are consistently found for yellow birch (Table 2.7, Figure 2.6)

and are different from the two other species in Marquette and Menominee. No differentiation can be made between CO values of sugar maple and eastern hemlock. Highest values of CO for both deciduous species are associated with the Menominee County, the region with the highest PET (Table 2.7).

2.6 Discussion

In an overall manner, parameters do not vary greatly between regions and patterns are most easily compared between species. This is in agreement with Wright et al. (1998) where a comparison of growth response to light for shade tolerant and intolerant species revealed differences across regions, but differentiation by species was still most important. It also supposes that important aspects of forest succession and dynamics are driven by species-specific traits and hence by interspecific differences (Canham *et al.*, 1994) over biophysical properties of sites.

For example, in eq. 1 sugar maple reaches superior heights than the other two species (the H1 values of sugar maple are lower than that of eastern hemlock but the slopes are higher (Table 2.3) so sugar maple reaches greater heights faster (Figure 2.3)). The greatest heights for sugar maple are associated with site fertility (Table 2.1), since this species has higher site indexes on sites with rich soils (Burns and Honkala, 1990). For sugar maple and eastern hemlock, height is the lower in regions at high latitude and increases for regions of low latitude, where degree-days and annual PET increase. This increase of height at the species southern limit is also observed for other species (Loehle, 1998). However, the present analysis shows that the order of regions differs among species.

Regarding equation 2, both tolerant species have generally high C1 values, which can represent the relatively wider crown of tolerant species (as opposed to intolerant) as saplings (Beaudet and Messier, 1998), eventhough our sample does not include saplings and these values are extrapolated. For eastern hemlock, the crown radius does not reach high values and is consistent between regions. This can be explained by its conic crown shape, as opposed to the ellipsoidal crowns of yellow birch and sugar maple.

Parameter C2, representing crown depth, also does not behave the same way among different regions. It can be observed in Table 2.5 that one C2 parameter of yellow birch is very high, while the curve (CDEXP) is low. This has for effect a very distinct relationship for the Marquette County. It can be explained by the considerable heights reached by yellow birch on this particular site, most of the individuals being between 20 and 30 meters high, for a relatively short crown. Therefore, the high value of C2, which represents a deep crown for saplings of 1m in height, is not representative of our sample, because data for saplings are extrapolated. Nevertheless, the reduced crown depth of mature individuals of yellow birch found in this region could reflect the effect of competition; in fact, the sites of this region do have a high mean basal area (Table 2.1). Species crown depth is also related to shade tolerance (Horn, 1971; Canham *et al.*, 1994), the more tolerant the species is, the more habilitated it is to keep shade leaves within an elongated crown. As a matter of fact, our most tolerant species, eastern hemlock, has CDEXP values not different from 1, indicating that crowns length linearly increases with total height.

The crown openness values obtained in this study generally correspond to previously published values (Canham *et al.* 1994, 1999; Beaudet *et al.*, 2002; Poulin

et al, 2004; Astrup and Larson, 2006) for tree species of North America. Both factors (species and region) had a significant effect on CO and are interacting (Table 2.6), which is in agreement with the results of Astrup and Larson (2006).

Yellow birch has consistently higher CO values, which indicates a more open crown compared to the two other species. This difference can be explained by the fact that sugar maple and eastern hemlock are shade tolerant species while yellow birch is considered mid-intolerant. Since Horn (1971) predicted that shade-tolerance was correlated to the species ability to intercept light, other studies confirmed this hypothesis (Canham *et al.* 1994, 1999; Beaudet *et al.*, 2002; Kitajima *et al.*, 2005), along with our results. However, for 3 regions out of 4, sugar maple has a higher CO than eastern hemlock. This result is in agreement with Horn (1971), but in not with Canham *et al.*, (1994). These discrepancies could be attributed to the different methods used for calculating crown openness.

Crown openness values are changing quite significantly between regions but these changes are not consistent within species. For both deciduous species, higher CO values are associated with the sites in Menominee County where the PET is the highest (Table 2.1). This suggests that a higher PET can reduce CO for these species, and in turn decrease their light interception capability. This result agrees with the assumption that foliage quantity and leaf size increase where water is more available (Zahner, 1968; Jose and Gillespie, 1996) and that PET is a controlling variable of leaf area Gholz (1982).

For the cases where the parameters of allometric equations differ greatly among regions for one species (such as eastern hemlock in eq. 1 and yellow birch in

eq. 2), the sample distribution (DBH range of selected individuals) or some stand characteristic such as an enhanced competition could be a cause. These factors should be considered as well as biophysical differences among sites. For example, the sites located in the Marquette County were younger stands, probably harvested in the early 20th century (Dean Long, personal communication). As a consequence, these sites had a structure closer to even-aged stands, where natural tree fall gap dynamics had not occurred yet. This could hinder the abundance of smaller yellow birch individuals, by limiting the high light conditions that are usually found in gaps (Burns and Honkala, 1990; Beaudet and Messier 1998; Webster and Lorimer, 2003). In some cases, variation in allometric parameters can be explained, but in other cases, external factors like site history were not controlled.

To examine the impact of the different allometric and light transmission parameters between regions, the model should be used to perform stand-level simulations. Outputs such as GLI maps could be used to compare how species create similar or different understory light environments depending on the region represented. This way, the assessment of the impact of such regional differences could be completed.

2.7 Acknowledgements

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2.8 Tables and Figures

2.8.1 Tables

Table 2.1 Summary of regional and site characteristics.

Region	Mean annual temperature (C°)	Annual evapotrans-piration (mm)	Sites coordinates	Mean CEC	pH	Soil texture	Humus type	Mean B. A. before harvest (m^2/ha)*	Mean density (trees/ha)*	Stand species composition**
Témiscamingue	4.4	556.3	46° 40' N, 78° 30' E.	2.00	4.43	loam	moder	23.3	525	SM, YB, EH.
			46° 37' N, 78° 08' E.	3.36	4.91	sandy loam	moder	16.3	525	SM, EH.
			46° 24' N, 78° 15' E.	2.99	5.03	sandy loam	moder	23.8	450	SM, YB, AB.
Haliburton	4.9	530.8	45° 14' N, 78° 37' E.	3.30	4.93	sandy loam	mor-moder	26.0	550	SM, EH, AB, YB.
			45° 14' N, 78° 37' E.	3.71	5.04	sandy loam	moder	24.4	492	SM, YB, EH.
			45° 21' N, 78° 32' E.	2.24	4.26	loam	moder	22.6	608	SM, BF, YB, EH.
Marquette	3.9	537.6	46° 20' N, 87° 19' E.	1.04	4.50	sandy loam	moder	32.5	525	SM, BC, YB, EH.
			46° 20' N, 87° 20' E.	0.66	4.26	sandy loam	moder	40.8	500	SM, YB.
			46° 20' N, 87° 17' E.	2.75	4.45	sandy loam	moder	38.5	617	SM, BC.
Menominee	5.5	559.8	45° 45' N, 87° 28' E.	6.54	5.91	clay loam	mull	27.9	667	SM, EH
			45° 45' N, 87° 35' E.	10.56	6,32	clay loam	mull	46.6	517	SM, YB, BF.

*for trees over 9 cm in DBH and including stumps in harvested plots.
** listed for each site in decreasing order of dominance: SM: sugar maple, YB: yellow birch, EH: eastern hemlock, AB: American beech, BF: balsam fir, BC: black cherry.

Table 2.2 Sample size of individuals selected for allometric measurement, and sub-sample size of individuals on which crown openness was determined as well, by each region and species (YB: yellow birch, SM: sugar maple, EH: eastern hemlock).

Region	Species	Allometry (n)	CO (n)	DBH range
Témiscamingue	YB	146	69	8.6-92.6
	SM	126	34	10.7-80.8
	EH	106	34	6.9-89.1
Ontario	YB	110	34	9.2-99.5
	SM	123	31	9.1-67.7
	EH	117	22	10.1-73.4
Marquette	YB	119	34	13-61.5
	SM	120	37	9.1-74-3
	EH	119	17	11.4-75.5
Menominee	YB	76	22	11.5-56
	SM	88	26	9.8-59.8
	EH	82	18	11.2-62.4
All sites	YB	451	159	8.6-99.5
	SM	456	128	9.1-80.8
	EH	423	91	6.9-89.1

Table 2.3 Parameter values (H1 and B), confidence intervals and r^2 for the Height-DBH relationship (see eq. 1).

Species	Region	*n*	H1	95% Low.CI	95% High CI	B	95% Low.CI	95% High CI	r^2
YB	Témiscamingue	142	23.13	22.05	24.28	0.057	0.049	0.065	0.589
	Ontario	110	22.53	21.03	24.03	0.091	0.071	0.110	0.379
	Marquette	119	23.64	22.73	24.54	0.089	0.073	0.105	0.348
	Menominee	76	26.16	23.38	28.95	0.053	0.039	0.067	0.489
SM	Témiscamingue	126	25.31	23.44	27.17	0.050	0.041	0.059	0.563
	Ontario	123	31.15	27.88	34.42	0.042	0.033	0.051	0.645
	Marquette	120	27.41	26.62	28.19	0.072	0.064	0.080	0.730
	Menominee	88	32.49	29.96	35.03	0.048	0.039	0.056	0.789
EH	Témiscamingue	104	26.87	24.15	29.58	0.027	0.021	0.033	0.843
	Ontario	117	32.17	27.83	36.52	0.023	0.018	0.029	0.833
	Marquette	119	28.66	22.86	34.46	0.021	0.014	0.028	0.662
	Menominee	82	40.57	27.96	53.19	0.016	0.009	0.023	0.744

Table 2.4 Parameter values (C1 and CREXP), confidence intervals and r^2 for the Crown radius-DBH relationship (see eq. 2).

Species	Region	*n*	C1	95% Low.CI	95% High CI	CREXP	95% Low.CI	95% High CI	r^2
YB	Témiscamingue	142	0.602	0.460	0.744	0.499	0.436	0.563	0.638
	Ontario	110	0.466	0.333	0.599	0.587	0.504	0.670	0.600
	Marquette	119	0.283	0.180	0.385	0.718	0.618	0.818	0.637
	Menominee	76	0.349	0.166	0.532	0.701	0.549	0.853	0.519
SM	Témiscamingue	126	0.768	0.469	1.067	0.398	0.287	0.510	0.287
	Ontario	123	0.5	0.363	0.638	0.564	0.485	0.643	0.628
	Marquette	120	0.27	0.174	0.365	0.734	0.639	0.829	0.694
	Menominee	88	0.820	0.529	1.111	0.442	0.338	0.546	0.476
EH	Témiscamingue	104	0.527	0.326	0.729	0.491	0.393	0.589	0.584
	Ontario	117	0.939	0.703	1.176	0.369	0.298	0.439	0.525
	Marquette	119	0.905	0.638	1.173	0.367	0.284	0.450	0.410
	Menominee	82	0.965	0.637	1.293	0.379	0.285	0.473	0.459

Table 2.5 Parameter values (C2 and CDEXP), confidence intervals and r^2 for the Crown depth-height relationship (see eq. 3).

Species	Region	*n*	C2	95% Low.CI	95% High CI	CDEXP	95% Low.CI	95% High CI	r^2
YB	Témiscamingue	142	0.431	0.233	0.629	0.999	0.849	1.153	0.561
	Ontario	110	0.116	0.010	0.221	1.418	1.118	1.717	0.489
	Marquette	119	2.375	-0.18	4.929	0.398	0.050	0.747	0.043
	Menominee	76	0.171	0.004	0.339	1.336	1.017	1.655	0.467
SM	Témiscamingue	126	0.25	0.088	0.412	1.185	0.971	1.398	0.525
	Ontario	123	0.221	0.122	0.320	1.263	1.122	1.404	0.725
	Marquette	120	0.298	-0.028	0.624	1.078	0.738	1.418	0.300
	Menominee	88	1.767	0.515	3.019	0.565	0.343	0.787	0.266
EH	Témiscamingue	104	0.527	0.308	0.745	1.025	0.887	1.162	0.807
	Ontario	117	0.6	0.430	0.770	1.024	0.929	1.118	0.845
	Marquette	119	0.582	0.421	0.742	1.052	0.954	1.149	0.817
	Menominee	82	0.894	0.558	1.229	0.889	0.764	1.015	0.750

Table 2.6 Summary of two-way ANOVA where the effect of region and species and their interaction on CO is tested.

Source	**df**	**Mean-Square**	***F*-ratio**	***P***
Region	3	314.5	13.6	<0.001
Species	2	661.6	28.6	<0.001
Region X Species	6	58.4	2.5	0.021
Error	301	23.2		

Table 2.7 Mean crown openness (%), standard error and sample size by species and region.

Species	Region	*n*	Mean CO	SE
YB	Témiscamingue	64	15.53[a]	0.76
	Ontario	20	13.03[b]	1.18
	Marquette	30	12.64[bc]	0.85
	Menominee	22	19.28[a]	1.36
SM	Témiscamingue	30	11.49[a]	0.85
	Ontario	20	10.22[b]	0.88
	Marquette	34	7.58[c]	0.47
	Menominee	25	13.46[ac]	0.78
EH	Témiscamingue	23	13.16[a]	0.77
	Ontario	13	10.99[b]	1.60
	Marquette	14	8.27[ab]	1.08
	Menominee	18	10.2[a]	0.77

Different letters following parameter value indicate that values are significantly different among regions for a given species ($P<0.05$).

Table 2.8 Summary of ANOVA for each region where the effect of species on CO is tested.

Region	Source		Mean-Square	*F*-rat	*P*
Témiscamingue	Species	2	177.7	6.219	0.003
	Error	114	28.6		
Ontario	Species	2	41.5	1.689	0.195
	Error	50	24.6		
Marquette	Species	2	220.2	15.110	<0.001
	Error	75	14.6		
Menominee	Species	2	430.5	19.091	<0.001
	Error	62	22.5		

2.8.3 Legends for figures

Figure 2.1 Measures of variables for each tree include DBH and a) crown width; b) total tree height; c) crown depth. Pictures were taken at 45°, 30°, 15° and 0° from zenith (locations represented by the black dots indicated on the d line).

Figure 2.2 Transformation and analysis of crown pictures in *Photoshop* (v. 7.0).

Figure 2.3 Height-DBH relationships for yellow birch (YB), sugar maple (SM) and eastern hemlock (EH), by regions. Solid line= Témiscamingue, long dash= Ontario, dot line= Marquette, short dash= Menominee.

Figure 2.4 Crown radius-DBH relationships for yellow birch (YB), sugar maple (SM) and eastern hemlock (EH), by regions. Lines represent the same regions as in Figure 2.3.

Figure 2.5 Crown depth-DBH relationships for yellow birch (YB), sugar maple (SM) and eastern hemlock (EH), by regions. Lines represent the same regions as in Figure 2.3.

Figure 2.6 Mean crown openness (±SD) per species for A) Témiscamingue, B) Ontario, C) Marquette and D) Menominee. Different letters indicate if mean CO values are different among species, within each region, according to a post-hoc Tukey test ($P<0.05$).

2.8.4 Figures

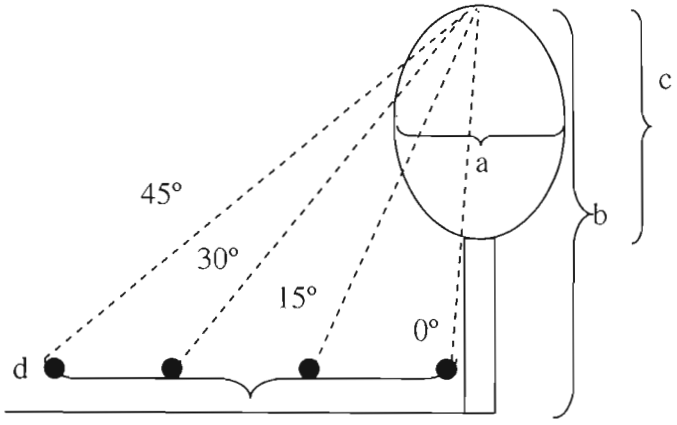

Figure 2.1

Figure 2.2

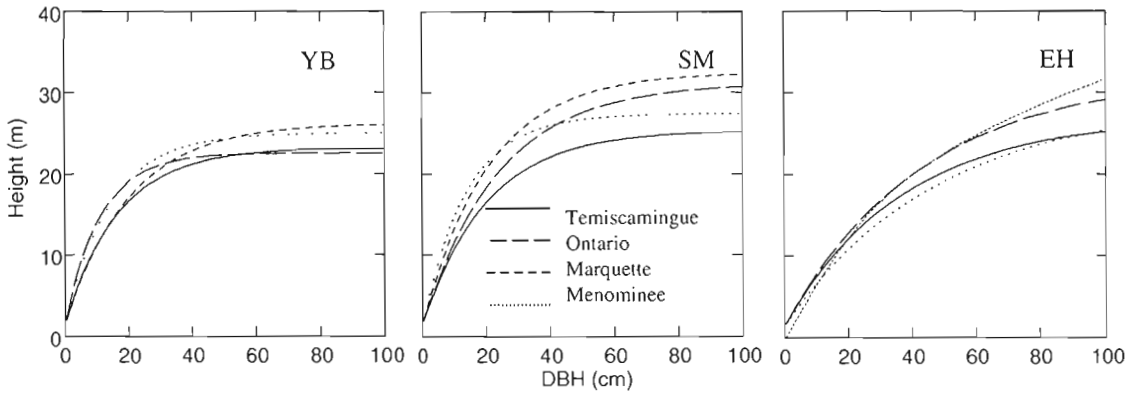
YB
SM
EH
Height (m)
DBH (cm)
Temiscamingue
Ontario
Marquette
Menominee
0
10
20
30
40
0
20
40
60
80
100

Figure 2.3

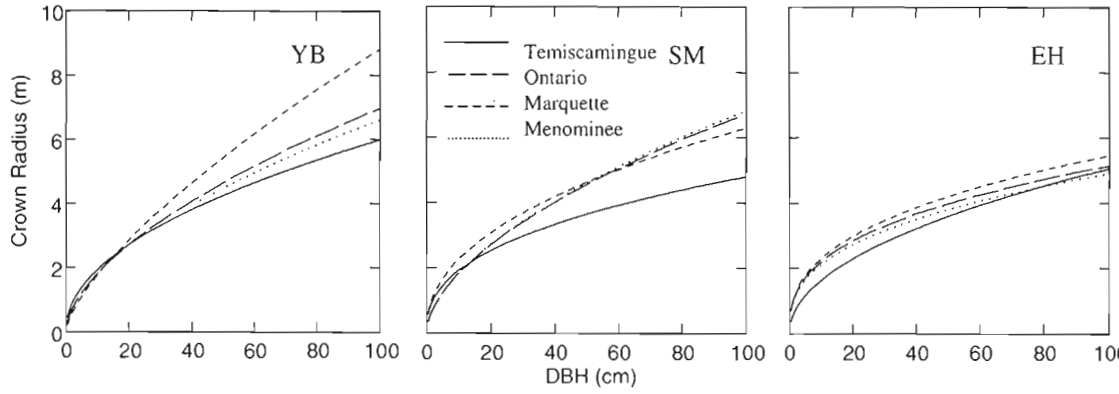
YB
SM
EH
Temiscamingue
Ontario
Marquette
Menominee
Crown Radius (m)
DBH (cm)
0
2
4
6
8
10
0
20
40
60
80
100

Figure 2.4

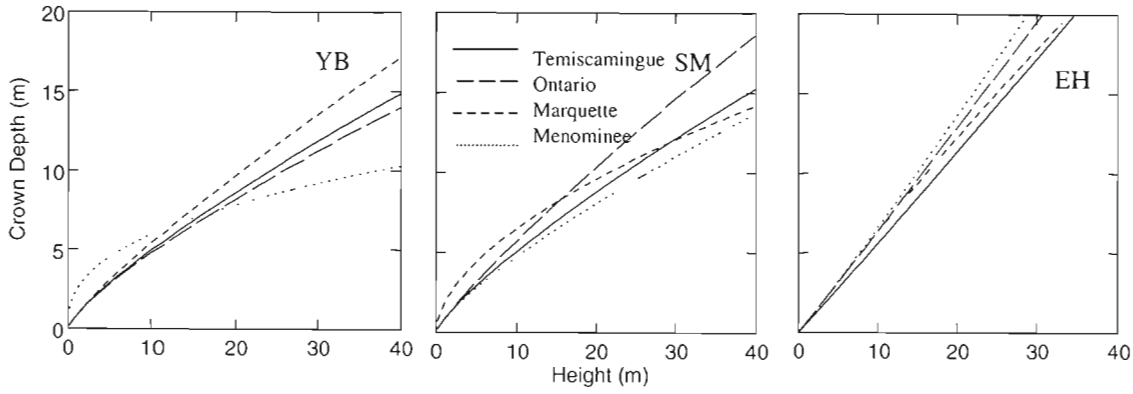
YB
SM
EH
Temiscamingue
Ontario
Marquette
Menominee
Crown Depth (m)
Height (m)
0
5
10
15
20
0
10
20
30
40

Figure 2.5

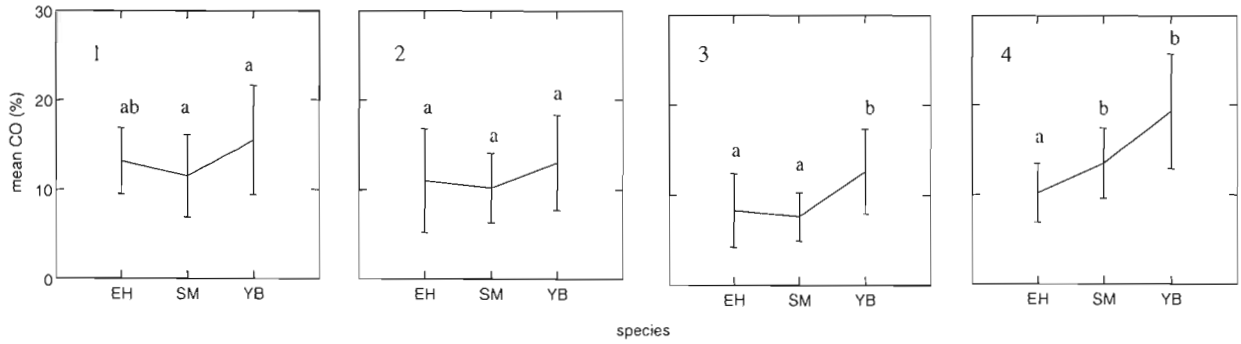

Figure 2.6

CONCLUSION GÉNÉRALE

Ce projet de recherche nous a permis de caractériser l'ouverture de la couronne et l'allométrie de l'érable à sucre, du bouleau jaune et de la pruche du Canada tout en tenant compte de la variabilité entre plusieurs régions de la forêt tempérée décidue dans le Nord-Est de l'Amérique du Nord. Les résultats obtenus nous permettent de conclure que :

1) Le bouleau jaune se distingue en n'interceptant pas autant de lumière que les deux autres espèces à l'étude. Les deux espèces tolérantes ne peuvent être différenciées au niveau de leur habileté à intercepter la lumière.

2) Les différences d'ouverture de la cime entre les régions étaient en partie attribuables à une variation de l'évapotranspiration chez les deux espèces décidues, mais cela n'était pas le cas chez le conifère. Dans le cas du bouleau jaune et de l'érable à sucre, le degré d'ouverture de la cime augmentait avec l'évapotranspiration.

3) Au niveau des couronnes individuelles, l'angle de transmission par rapport au zénith, le DHP ainsi que le ratio diamètre de la couronne/diamètre au tronc (un indice de suppression/dominance) semblent influencer grandement l'ouverture de la couronne, surtout chez les espèces décidues. En ce sens, on observe que les individus avec un fort indice de suppression, ne peuvent capter la lumière de façon efficace latéralement. Les arbres dominants sont habiletés à intercepter la lumière latéralement et horizontalement.

4) La paramétrisation du module de lumière de SORTIE a permis d'observer certaines différences entre les espèces et les régions pour les paramètres allométriques et l'ouverture de la couronne. Concernant les paramètres d'allométrie, les quelques différences interrégionales peuvent être expliquées par les particularités de l'échantillon ou l'historique du site. Il est possible que les paramètres allométriques

puissent être généralisés pour une espèce à l'intérieur d'un biome si 1) les peuplements se ressemblent dans leur structure et leur historique et si 2) l'échantillon comprend un nombre élevé d'individus de grandeurs variables.

5) Les valeurs d'OC ne peuvent être généralisées pour un biome puisque celles-ci varient selon les régions (particulièrement selon l'évapotranspiration, conformément aux résultats du chapitre 1).

Nous démontrons par cette étude l'importance de considérer différents facteurs affectant l'ouverture de la couronne ainsi que variations interrégionales au niveau des relations allométriques des trois espèces à l'étude. Nous n'avons toutefois pas évalué dans le cadre de ce projet de recherche dans quelle mesure le fait de tenir compte ou non de ces sources de variation aurait un impact sur la prédiction de la lumière à l'aide de modèle de simulation comme SORTIE (module de lumière). Les prochains travaux devraient porter sur la quantification des effets de variations (de la magnitude observée dans la présente étude) dans les valeurs d'ouverture de la couronne et l'allométrie des arbres en utilisant le modèle SORTIE. En simulant la transmission de lumière en se basant sur les paramètres obtenus pour les différentes régions, nous serons en mesure de voir l'effet de ces paramètres sur les prédictions. Ainsi, nous pourrons observer les changements qui pourraient survenir lors d'une hausse en évapotranspiration, comme il est prévu dans le cadre du réchauffement global, et évaluer les risques associés à celui-ci.

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